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OBSERVATIONS ON THE NESTING BEHAVIOR OF THREE SPECIES OF *PLENOCULUS* FOX (HYMENOPTERA: SPHECIDAE)

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Plenoculus Fox is a little studied genus of relatively small fossorial wasps known predominantly from the desert regions of the New World. Detailed biological data exist for a single species, *P. davisi* Fox, where females are known to construct shallow, multicellular nests which they provision with both adult and immature hemipterans, primarily of the family Miridae (Williams, 1960; Evans, 1961; Kurczewski, 1968). Published prey records for *P. stygius* Williams and *P. propinquus* Fox similarly indicate the use of Hemiptera (Kurczewski, 1968). *P. cockerelli* Fox, however, was observed by Williams (1960) to utilize larval Lepidoptera "resembling pyralids." In the present paper we further elucidate the nesting biology of *P. propinquus, P. cockerelli,* and a second species preying on larvae of Lepidoptera, *P. boregensis* Williams from New Mexico.

Study Areas

Both *P. cockerelli* and *P. boregensis* were found nesting in the La Joya State Game Refuge, which lies in the Rio Grande Valley midway between the New Mexican towns of Belen and Socorro. Bordered on the western side by an extensive dune field, and occupying the marshland of this section of the river valley, the La Joya refuge contains a number of unique habitat conditions especially conducive to the nesting of a wide diversity of digger wasps. Surrounding this smaller refuge is the much larger, newly created, Sevilleta National Wildlife Refuge, which affords many other semi-arid habitat types, including the remainder of the mentioned dune field.

P. propinquus, the third species included in the present study, was observed at two locations. Some nesting data and prey records were collected at the Great Sand Dunes National Monument in southern Colorado in August, 1978. Additional prey records were obtained from specimens collected by G. E. Bohart and P. Torchio at Cornish, Utah (wasps pinned with prey), and from a population studied at La Porte, Colorado in June and July, 1979.

Ethology

I. *Plenoculus cockerelli* Fox. The two relatively compact New Mexican aggregations of this wasp which we studied were restricted to well isolated, nearly level, hard packed, fine sandy soils beside a primitive dirt road leading into the northern portion of the La Joya Refuge. A thin, dry surface crust was present to a depth of approximately 0.5–1 cm on the nesting area and subsurface conditions were relatively moist, a result of the proximity of marshes and holding ponds which maintain the water table at a high level in the immediate area. In addition the continuous evaporation from the soil surface also imparts a visibly saline nature to the soil surface. Nesting in the same site were also *Tachytes aurulentus* (Fabricius), *Cerceris bicornuta* (Guerin) (Evans and Rubink, 1978), and *Oxybelus* sp.

Observations of *P. cockerelli* are based on two years of intermittent study. Peak levels of nesting activity at the sites varied considerably. In 1976 extensive nesting activities were recorded in mid-July, while in 1977 nesting was completed by late June; no wasps were observed nesting in late summer either year. This single peak of nesting activity observed each year suggests that this species is univoltine in nature at La Joya.

Nesting behavior in this species is similar in many respects to that described by Kurczewski (1968) for *P. davisi.* Selection of a specific location for a new nest involves flying just above a small area, landing on the soil surface repeatedly, and biting the soil at prospective nest locations. In one of the two examples of nest site selection observed, the nest was begun immediately after, and within 20 cm of a previous nest. When a suitable site is discovered, nest construction begins. Removal of excavated material is accomplished by pushing large quantities of loosened soil in a manner similar to the technique described for *P. davisi* (Kurczewski, 1968). Occasional leveling activity interspersed with removal of excavated soil prevents the accumulation of a tumulus at the nest entrance. In the two cases where nest initiation was observed, less than one hour intervened between the selection of a nest site, temporary closure, and bringing of the first caterpillar prey item to the nest.

The nest architecture of one of the ten successfully excavated nests is depicted in Fig. 1. Most nest construction activity occupied the late morning hours (1000–1200 hours), although a limited amount of leveling activity outside new nests was also observed in the afternoon (1500–1700 hours). Nest provisioning begins in the mid-morning hours (0900–1000 hours) and continues incessantly throughout the morning and early afternoon. By approximately 1600 hours very little activity is visible in the nesting area.

Prey are transported to the general vicinity of nest in flight, grasped by the middle legs of the wasp. Upon landing, the wasp carries the prey along the soil surface to near the nest entrance. She then deposits the prey tem-

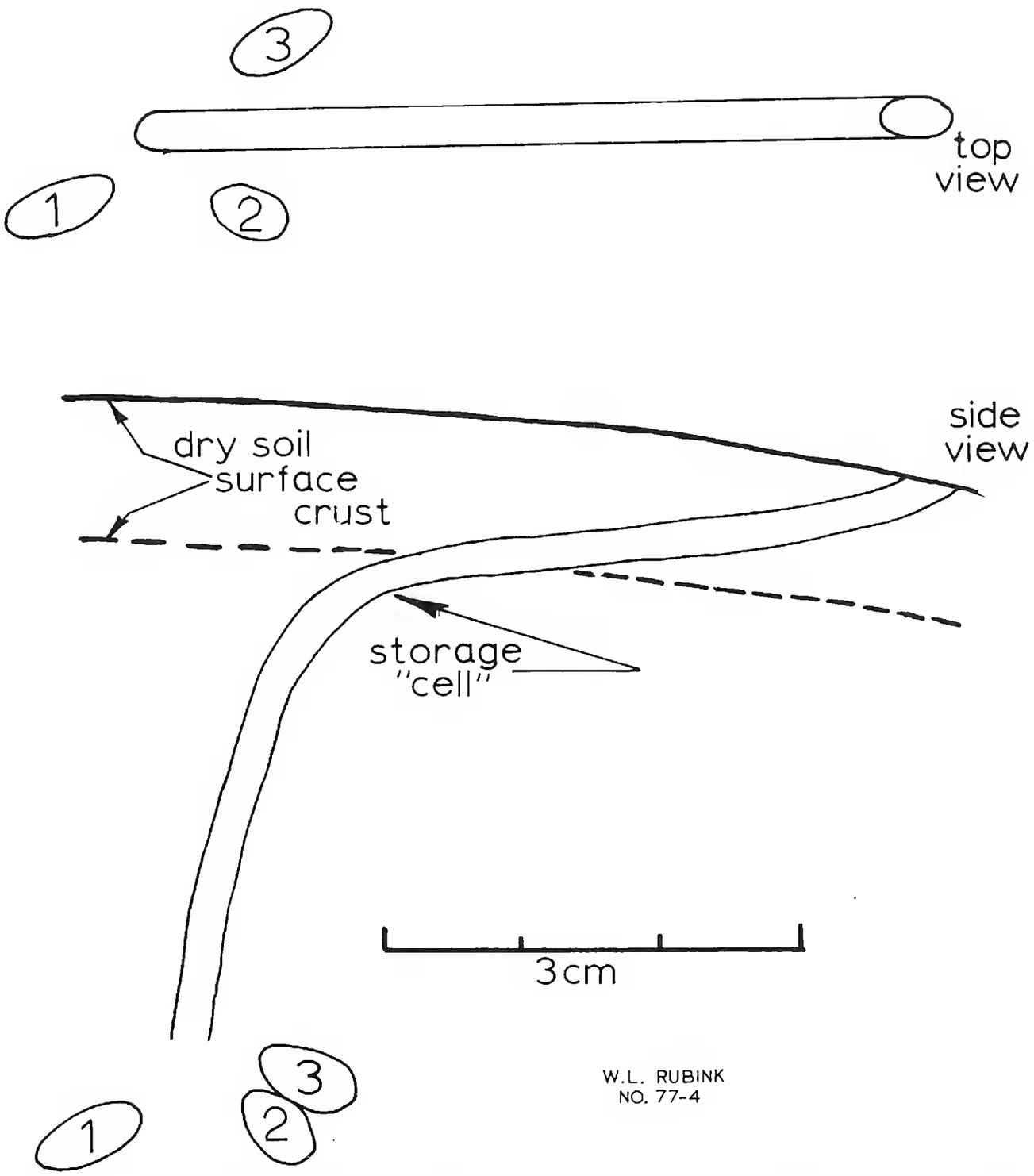

Fig. 1. Nest diagram showing architecture of an active nest of *Plenoculus cockerelli*. See text for further explanation.

porarily at that location and, using her forelegs to scrape away the temporary closure of earth, opens the nest. She then enters the burrow, turns around inside, reemerges momentarily to grasp the prey with her mandibles, and then backs into the burrow with it. The burrow is not closed from within.

Two nests examined during the period of active provisioning by the wasp

Table 1. Summary of prey records of *P. cockerelli, P. boregensis,* and *P. propinquus*. Records for the first two species represent lepidopterous prey exclusively.

Identity of prey items	Distribution (no. of specimens)	Location
	Plenoculus cockerelli Fox	
Gelechiidae		
Filatima sp.	9	La Joya Game Refuge
Aristotelia sp.	9	La Joya Game Refuge
Noctuidae		
Tarachidia sp.	6	La Joya Game Refuge
Momphidae		
Sorhagenia sp.	3	La Joya Game Refuge
Lyonetiidae		
Buccalatrix sp.	1	La Joya Game Refuge
	Plenoculus boregensis Williams	
Gelechiidae		
Aristotelia sp.	23	La Joya Game Refuge
Noctuidae		
Tarachidia sp.	1	La Joya Game Refuge
	Plenoculus propinquus Fox	
Miridae (Hemiptera)		
Lygus sp.	20	La Porte, Colorado
Philophorus hesperus Knight	1	Great Sand Dunes Nat. Mon.
Philophorus sp.	1	Great Sand Dunes Nat. Mon.
Deraecorus sp.	1	Great Sand Dunes Nat. Mon.
Ceratocapsis sp.	1	Great Sand Dunes Nat. Mon.
Unidentified Orthotylinae	1	Great Sand Dunes Nat. Mon.
Unidentified nymphs	11	Great Sand Dunes Nat. Mon.
Mirinae nymphs	2	Cornish, Utah

revealed that the prey items are stored not in the cell, but midway down the burrow at the point where it begins a steeper descent. Neither nest contained an empty cell, so presumably cell construction takes place after the wasp has collected a suitable number of prey.

Two nests excavated late in the afternoon of the same day on which they were begun each had a single completed cell which contained several prey items. The entrance to the cell was already filled and in both cases the female wasp was found in the burrow at the top of the filled material. Older nests or nests of undetermined age contained from one to three cells and contained from one to six prey items per cell ($\bar{x}$ + S.D. = 3.3 ± 1.5, N =

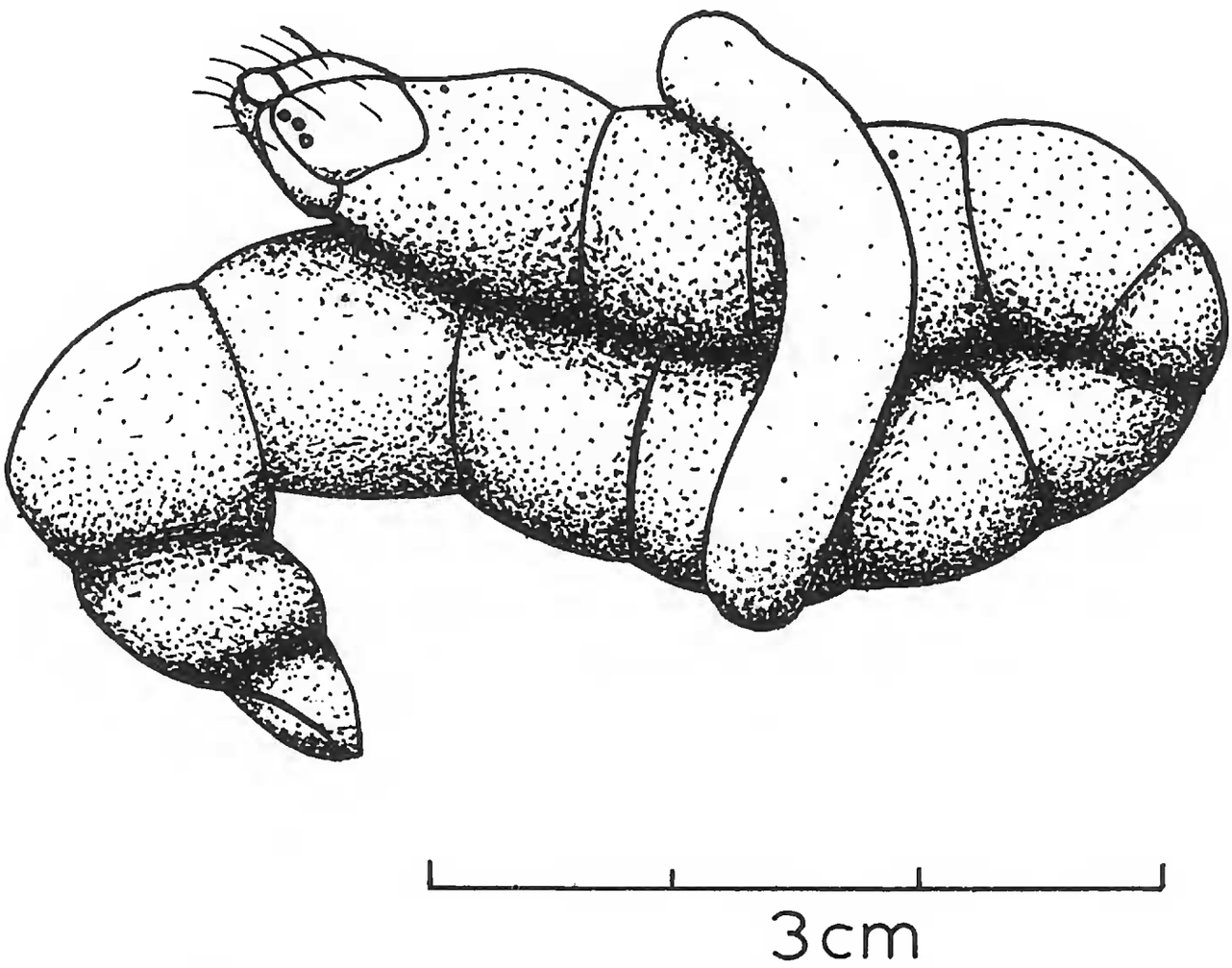

Fig. 2. Position of the egg on the lepidopterous prey item of cell number 3 of the nest of Fig. 1. See text for further explanation.

15). Prey of *P. cockerelli* were from five genera of larval Lepidotera belonging to four families (Table 1). The egg was always laid on the last contents placed in the cell (the prey item or items nearest the traceable portion of the burrow and presumed cell entrance); however, the position of the egg on the prey varied. In two of the 5 cases where it could be ascertained, the egg overlapped one or more of the variously folded prey items (Fig. 2). In the other cases it was laid more or less longitudinally on a single caterpillar. No parasites were recorded for this species, although a single tachinid egg was found on one of the prey items. Males of this species were not observed; one specimen was recovered from a nearby malaise trap.

II. *Plenoculus boregensis* Williams. This species nests widely throughout the active dune areas of both the Sevilleta and La Joya Refuges in New Mexico. In both 1976 and 1977 nesting activities of *P. boregensis* were recorded as early as July. Early in the season it forms loose aggregations in the vegetation-free, gently sloping (10–20% slope), expanses of open sand found in blowouts and between dunes. These early season nests occupied

much the same area as that used by a large aggregation of *Bembix pallidipicta* Smith. In the late summer and early fall (August–September) more compact nesting aggregations are formed on more southernly, and slightly steeper (20–40%) slopes.

Prey transport is identical to that described for *P. cockerelli*. In contrast to *P. cockerelli, P. boregensis* is either bi- or multivoltine in the study area. This was determined by sifting the sand in known early and late season nesting aggregations after all 1976 nesting activity had ceased (in March 1977). In the early season nesting area only empty cocoons were discovered, while in the late season nesting site more than 300 intact cocoons (most containing diapausing larvae or prepupae) were found. A large number of these were reared in the laboratory.

The successful, complete excavation of two nests and the partial excavation of several others provided meager information concerning nest architecture in *P. boregensis*. Nests are relatively shallow. In the two excavated nests where cells were found the burrows angled into the soil at approximately a 45° angle to 10 cm depth and terminated abruptly in a cell. One of these nests contained a second cell at approximately 15 cm depth, directly below the first cell. Nest structure is thus superficially similar to that of *P. cockerelli*. This is further exemplified by the observations from several incipient nests in which the caterpillar prey were found stored, not in the cell, but in the burrow at a point several centimeters from the burrow entrance.

Numerous prey records obtained from successfully excavated nests, storage areas, or abandoned on the surface indicate a remarkable specificity (Table 1). A single record of non-*Aristotelia* prey was obtained in 1976 from a female as she was carrying it to the nest. Egg position on the prey was not observed in this species.

Forty-four wasps emerged from cocoons collected in the field in March, 1977 (1976 nesting season) and brought to the laboratory for rearing. The sex ratio of emerging adults was not significantly different from 1:1 (χ^2 = 0.86, d.f. = 1; χ^2 = n.s.; F/M = 0.75:1). Malaise trap sampling in both dunal and marsh habitats yielded both males and females. Sex ratios from this sampling during the 1976 nesting season produced a significantly female biased sex ratio (χ^2 = 26.90; d.f. = 1; $P < 0.005$; F/M = 2.28:1). Four male mutillid parasites (*Photopsis* sp.) were reared from the cocoons of *P. boregensis*. No other parasites were found, but myrmeleontid larvae that lay in wait near the soil surface were observed to prey upon adult males. Tsuneki (1956) has also reported this for Japanese *Bembix*.

P. boregensis males are abundant in the female nesting areas throughout the nesting season where they actively alight on the soil surface and investigate open burrows and depressions in the sand, presumably in search of females. Two copulations were observed in nesting area in September, 1976.

In each case the male encountered a female as she was digging a nest. Grappling ensued and they rolled along the ground for a few seconds. After the struggle ceased the male perched on the dorsum of the upright female for 10–20 seconds before flying away.

III. *Plenocolus propinquus* Fox. This species was found nesting in well isolated, compacted, sandy soils of the Great Sand Dunes National Monument, and in well isolated, relatively less compacted soils north of the Cache la Poudre River in La Porte, Colorado. Both sites are located on level terrain, although a single female captured with prey at La Porte was apparently nesting in the relatively steep cut of a sand bank. Typical nest architecture is depicted in Fig. 3. Digging commences in late morning (actual nest site selection was not observed) and extends into the early afternoon. Limited observations suggest that as many as two cells may be completed in a single day. A tumulus does not accumulate at the nest entrance due to the progressive leveling during construction.

Prey are carried in flight to the nest head forward, venter up and grasped by the middle legs of the wasp. In a number of cases, as the wasp landed near the nest entrance, it could be seen to partially release its hold on the prey item with its legs, thus demonstrating that the mandibles are also used in prey carriage. Apparently the wasp grasps the beak of the hemipteran, as *P. davisi* has been reported to do (Evans, 1961; Kurczewski, 1968). From three to five prey items were stored per cell ($\bar{x} \pm$ S.D. = 3.5 ± 0.8, N = 10). Prey at the La Porte location were consistently adults of the genus *Lygus*; however, several mirid genera of both adults and immatures were used by the Great Sand Dunes population (Table 1). Egg position is identical to that described for *P. davisi* (Kurczewski, 1968). Two larvae of this species were brought to the laboratory in late June for observations of cocoon spinning behavior. Both of these larvae spun their cocoons on July 14 and emerged on July 28. This indicates that *P. propinquus* is at least bivoltine at the La Porte location.

Discussion

The addition of data on prey specificity in *Plenoculus* provides support for Williams (1960) separation of the genus into two species groups based on the presence of an emarginate, dentate clypeus (especially in the females) in the species which prey on hemipterans (the "*P. propinquus* group"), and a gently outbowed to cuneate, edentate clypeus in those species preying on larval Lepidoptera (the "*P. cockerelli, P. parvus* group"). The fact that both *P. propinquus* and *P. davisi* have been observed to utilize the mandibles in prey carriage (Evans, 1961; Kurczewski, 1968) leads to the suggestion that the emarginate clypeus is actually an adaptation to facilitate grasping the beak of the hemipterous prey item. The outbowed to strongly cuneate clypeus of the second species group can also be interpreted as a more efficient

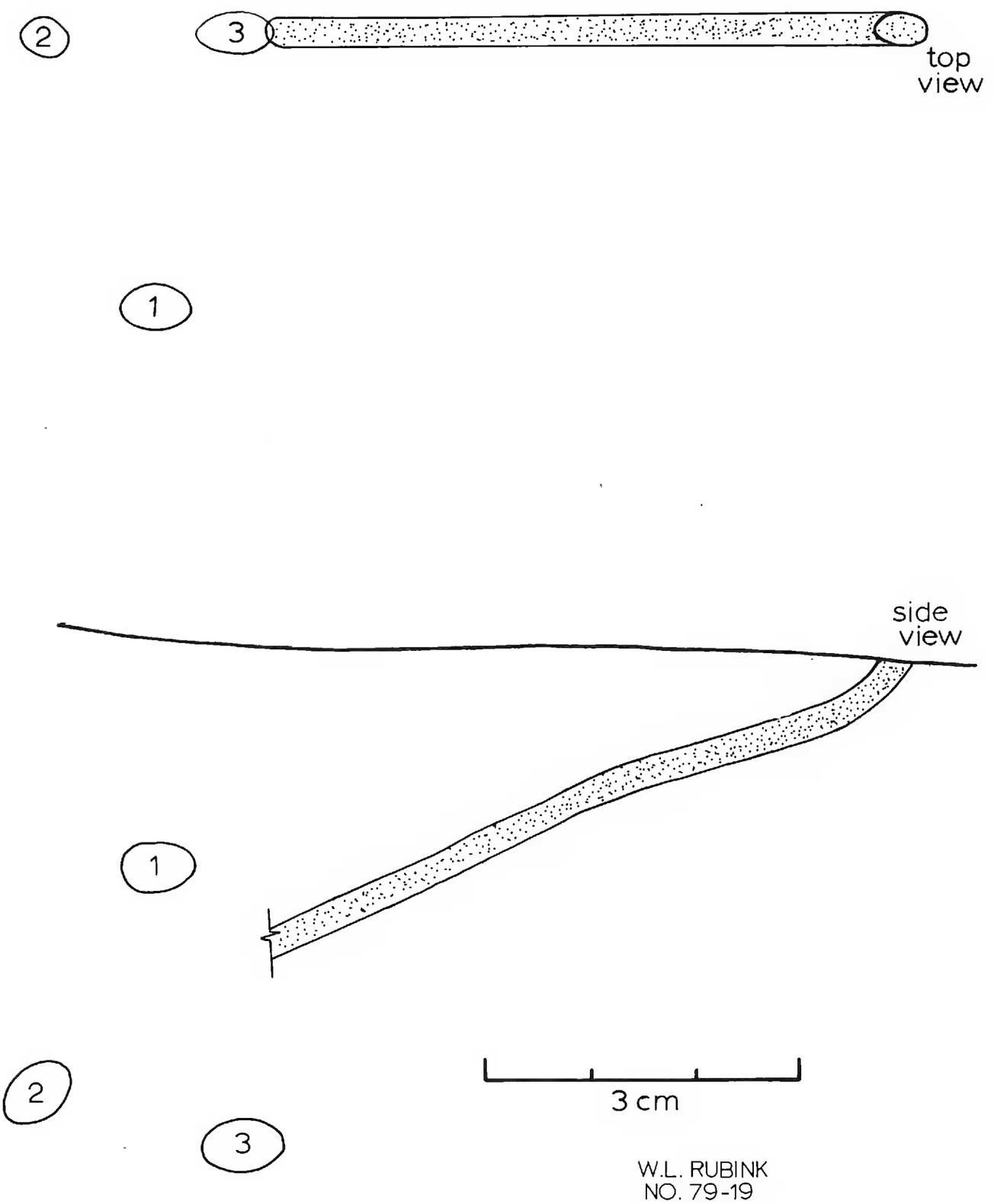

Fig. 3. Nest diagram depicting the architecture of a typical nest of *Plenoculus propinquus* after final closure.

mechanism for handling the soft-bodied, Lepidopterous prey items. The downward projecting clypeus would further aid the mandibles by holding the prey item tightly against them. Thus, although Williams (1960) considered *P. boregensis* to be rather intermediate in position, its use of lepidop-

terous prey would seem to link it more closely to the "*P. cockerelli, P. parvus*" species group than to the *P. propinquus* group. Male genitalic differences further support this contention (Rubink, unpublished notes). In addition, a third species of the *P. cockerelli* group from Southern Texas (undescribed, but close to *P. cuneatus* in Williams' key) has a strongly cuneate, edentate clypeus and also preys on larval lepidoptera (Rubink, unpublished observations).

The two species groups of *Plenoculus* differs in yet another way. In all the species we have observed thus far to prey on Lepidoptera they consistently make temporary closures when in search of prey. However, neither *P. davisi* nor *P. propinquus* have been observed to make temporary closures during periods of active provisioning (Evans, 1961, Kurczewski, 1968). Whether this results in differences in the incidence of parasitism is not known.

Habitat and prey preferences of *P. cockerelli* and *P. boregensis,* found nesting within a few hundred meters of each other at the La Joya site show striking differences. *P. cockerelli* is a more ephemeral species. Yearly activity is limited to a relatively short time span, and it is univoltine. Interestingly, it is also more of a generalist in its selection of lepidopterous prey items. This presumably results from non-selective hunting in a variety of habitats. *P. boregensis,* on the other hand, is probably bivoltine and active the entire summer. It, too, does not limit its activities to areas immediately adjacent to the nesting site, but is commonly found on flowers in the same habitat as *P. cockerelli.* In spite of this *P. boregensis* seems to have specialized on a narrow range of prey species.

The Hemiptera-preying species *P. propinquus,* based on the large variety of prey items, both adults and immatures, taken at the Great Sand Dunes site, also seems to be somewhat of a generalist although it preyed on only a single species of *Lygus* at the La Porte site. Thus, among the species of *Plenoculus* for which sufficient prey records are available (*P. cockerelli, P. boregensis, P. davisi,* and *P. propinquus*), only *P. boregensis* seems to be narrowly specialized.

Acknowledgments

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Footnote

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NOTICE

The Seventh International Symposium on Plecoptera will be held August 19–22, 1980, at the Nara Women's University in Nara, Japan.

The Plecoptera meetings are being held in conjunction with the XVI International Congress of Entomology (Kyoto, 3–9 August 1980) and the XXI Congress of the International Association of Theoretical and Applied Limnology SIL (Kyoto, 24–31 August 1980).